

OCCURRENCE AND GROUP ORGANIZATION OF ATLANTIC BOTTLENOSE PORPOISES (*TURSIOPS TRUNCATUS*) IN AN ARGENTINE BAY

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While the social behavior of many terrestrial mammals has been well described (see Wilson, 1975, pages 456-546, for a review), much less is known about the social organization of the several species of porpoises that inhabit all oceans of the world (Norris and Dohl, 1978a, provide a review). This lack of information results from the difficulty of remaining with a group of porpoises in the open ocean long enough to observe the details of porpoise behavior, and from the interference with the animals' behavior that a boat causes.

There are places where porpoises come close enough to shore to make observations from land feasible (Mitchell, 1975). Saayman, Bower, and Tayler (1972) described the activity cycles and movements of Indian Ocean bottlenose porpoises and Indopacific humpback porpoises by observations from South African cliffs; and Norris and Dohl (Norris, 1974; Norris and Dohl, 1978b) made similar observations on Hawaiian spinner porpoises from shore vantage points. In the present study, Atlantic bottlenose porpoises were observed from a 45-meter cliff located on the coast of south-Argentina. The purpose of this paper is to describe the seasonal pattern of occurrence, group stability, surfacing associations, and calving seasonality of these animals. These data represent a first step in understanding the social behavior of the bottlenose porpoise. Some information on the group stability of this porpoise population and the photographic technique used to gather these data has been presented elsewhere (Würsig and Würsig, 1977). The present paper is a more complete treatment of this material.

MATERIALS AND METHODS

During a 21-month stay, from July 1974 through March 1976, at Golfo San José (42° 23' S, 64° 03' W), bottlenose porpoises, *Tursiops truncatus*, were observed as they periodically passed within one kilometer of a shore observation point (camp). To investigate the group composition and stability of this population, porpoises were identified by photographing the natural markings on the trailing edges of their dorsal fins (see Würsig and Würsig, 1977). Observations lasted from ten minutes to several hours, depending on the length of time that the porpoises stayed near shore. It was assumed that all porpoises were photographed when each animal was identified at least four times within the record of one photographic observation session.

In the present paper, *group* refers to 53 individually identified bottlenose porpoises which passed through the study area during a 21-month period. This group

is part of a larger population of unknown size. *Subgroup* refers to those animals of the group which passed by shore at any one time.

To assess surfacing associations of animals, a motordrive Nikon camera was used. This provided data not only on which individuals were present, but also on their dive times and on which individuals surfaced together. To collect this information, a photograph was taken each time one or more animals surfaced (up to 1.5 frames/sec could be taken). The camera clicks were recorded on magnetic tape, and comparison of times between photographs and the individuals recognized in those photographs provided individual dive times and a measure of whether any animals tended to surface at nearly the same time. The technique can be profitably used when the animals are close enough to the camera to allow for recognition of all individuals as they surface. The use of a 35 mm motordrive camera provided large negatives with the detail necessary for recognizing individual animals; yet the rate of picture taking was sufficient to photograph all animals as they surfaced. A ciné-camera technique for determining group size, deployment, and speed (but not recognition of individuals) was described by Tayler and Saayman (1972a).

Seasonal occurrence patterns were analyzed using analysis of variance (Sokal

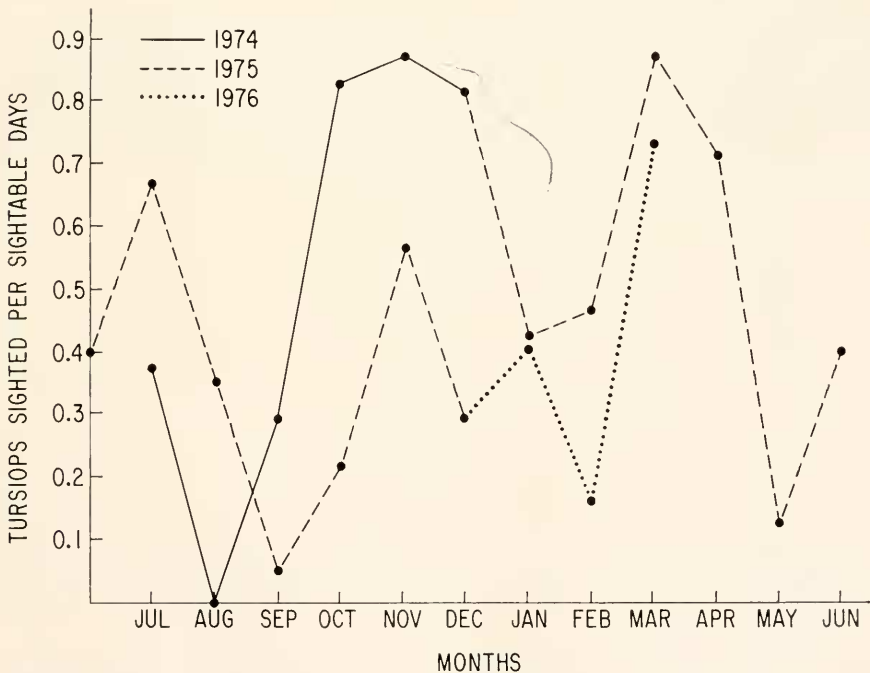


FIGURE 1. The fraction of the possible days each month on which bottlenose porpoises were sighted. The Y-axis represents the ratio of the number of days on which porpoises were sighted divided by the number of days each month with winds less than 20 km/hr. July, November, and March were months of maximum porpoise sightings; in September, February, and May they were sighted significantly less ($P < 0.001$, analysis of variance, Sokal and Rohlf, 1969, pages 204-249, and Rohlf and Sokal, 1969, pages 168-197).

and Rohlf, 1969; Rohlf and Sokal, 1969), surfacing associations were tested with a sampled randomization test (Sokal and Rohlf, 1969), and significance of calving seasonality was obtained with the Raleigh test, using the procedure described by Greenwood and Durand (1955).

RESULTS

Seasonal occurrence pattern

On days with winds greater than 20 km/hr it was difficult to see or photograph porpoises. Of the 433 days with winds less than 20 km/hr, bottlenose porpoises were seen on 191 days, or 44% of the days on which observations were made. The number of days on which porpoises were sighted varied greatly from month to month. As Figure 1 shows, porpoises were seen near shore during 20 of the 21 months studied; August, 1974, was the only month without sightings. But the number of days on which they were sighted varied greatly from month to month: there was a peak of abundance about every four months, and this pattern was similar for the two years.

Subgroup composition and stability

Bottlenose porpoise subgroups were photographed on approximately 150 of the 191 sighting days. There are 35 days on which all individuals in a subgroup were photographed at least four times. Figure 3 shows which of the 53 known individuals were present on each of these 35 days. Only one subgroup was sighted during any one day. The number of individuals in a subgroup varied from eight to 22, with a mean of 14.9 (s.d. = 3.28, see Figure 2).

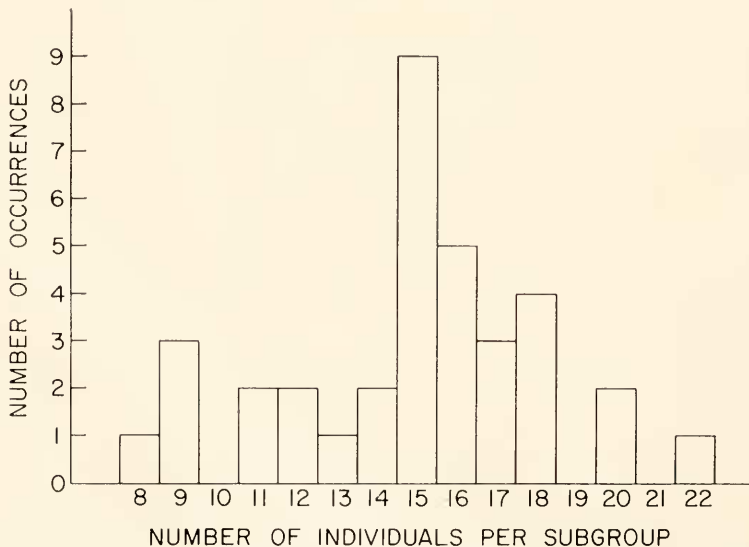


FIGURE 2. A histogram of subgroup sizes during 35 days on which all individuals present were recognized.

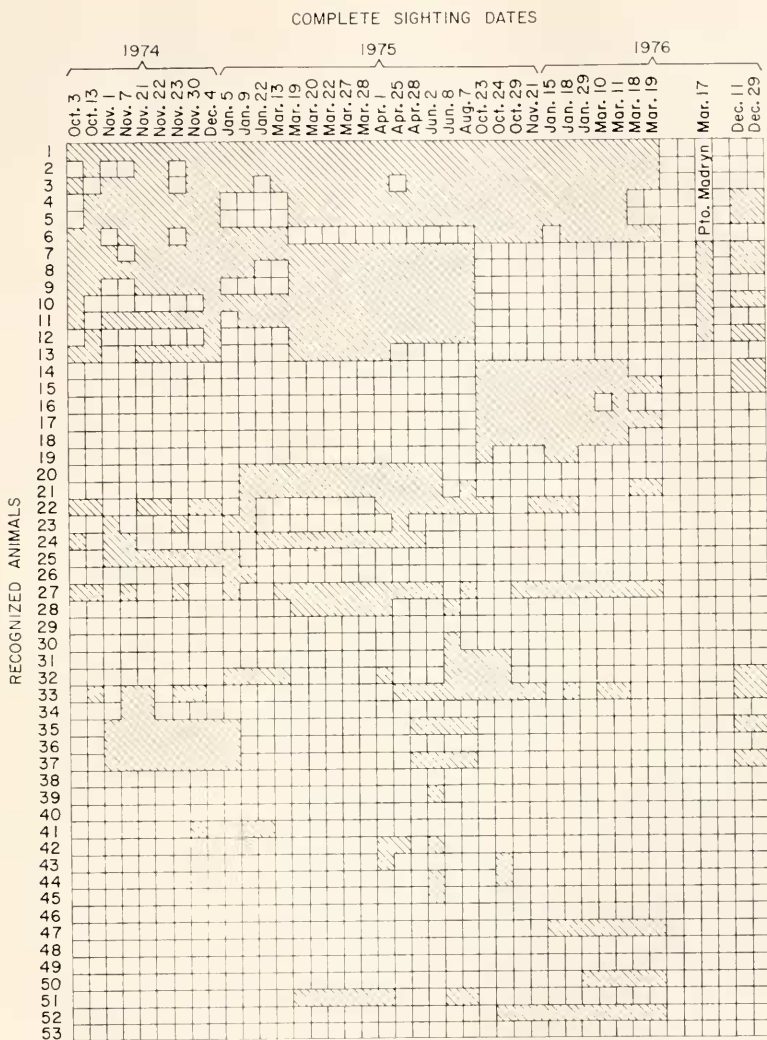


FIGURE 3. Specimens of *Tursiops* recognized during a 21-month continuous study period. Shaded blocks represent the presence of individuals during 35 complete sighting days (see text). The last three shaded columns on the right represent additional sightings of animals first at 300 kilometers removed from camp, and, secondly and thirdly, animals found near camp December, 1976.

As Figure 3 makes clear, this variation in subgroup size was the result of a continual flux of animals leaving and joining the subgroups. Nevertheless, some animals, namely #1-5, may be termed "core" animals since they were present throughout the study period. Animals #7-12 were present during the first ten months but subsequently disappeared during the month when animals #14-18 first appeared. In addition to these major changes in subgroup composition other

individuals appeared and disappeared together. For example, #2, #9, #13, and #22 disappeared between October 13, 1974, and November 21, 1974, while #24 appeared during their absence. At that time as well, four others (#25 and its calf #36, #35, and #37) appeared and stayed until January 5, 1975. From January 5, 1975, to March 19, 1975, five animals (#4 and its calf #5, #9, #12, and #13) disappeared while once again an individual (#32) appeared in their absence. When these five reappeared and #32 disappeared March 19, two new animals appeared (#28 and #51). Porpoises #51, #28, and #13 disappeared again by April 25, 1975. Porpoise #6, which was absent from March 19 to October 23, 1975, reappeared with the large shift in individuals first documented on that date. A monthly summary of the presence and absence of 22 of the animals described above is shown in Figure 4. The appearance and disappearance of other animals was apparently not related to the presence or absence of conspecifics.

Porpoises #7-12, which disappeared from camp in September 1975, were spotted in March, 1976, over 300 kilometers from the study site. On December 11 and 29, 1976, after nine months of no observations, a spot-check of porpoises near

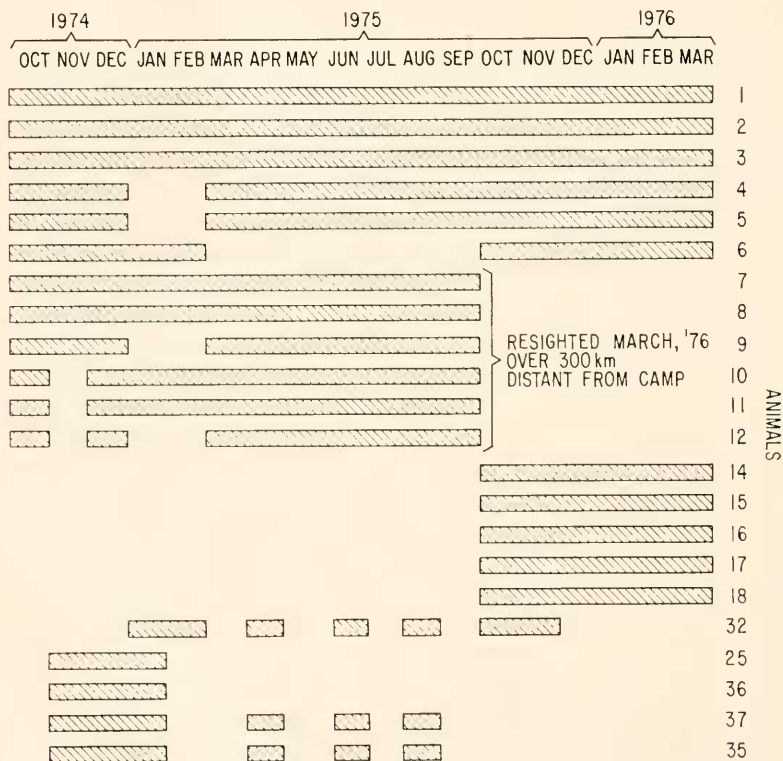


FIGURE 4. A month-by-month summary of the presence of 22 individuals which show interpersonal relationships in presence or absence within a subgroup. Differences in the summary and Figure 3 are due to consideration here of all sighting days, while Figure 3 represents only the 35 complete sighting days when all individuals were recognized.

TABLE I

Pairs of porpoises surfacing within three seconds of each other on two days in January, 1976 [(ns) = not surfacing significantly together; probability of random occurrence, $P < 0.025^$, or $P < 0.001^{**}$, sampled randomization test].*

January 18, 1976	January 29, 1976
#4-#5**	#4-#5**
#3-#52*	#3-#52 (ns)
#2-#6*	(only #6 present)
#2-#52*	(only #52 present)
#27-#6*	#27-#6 (ns)
#6-#18*	#6-#18 (ns)
#4-#27 (ns)	#4-#27*
(only #52 present)	#52-#50**

camp showed that four of these six animals were again in the original study area. At that time, 12 of the 53 known animals were present but no new animals were recorded. Interestingly, of the core unit of five animals, only #4 and #5 were present, suggesting that even the "core" may not be stable over a larger time period.

Surfacing associations and dive times

To determine whether there is any association between animals breathing together which might indicate a social bond, the surfacing pattern of porpoises was examined for two days in January, 1976. As Table I shows, while adult-adult surfacing associations occurred, they were not the same associations during the two sampled days, and they were never of greater significance than at the $P < 0.025$ level (sampled randomization test, Sokal and Rohlf, 1969, p. 633). Adult-calf associations, however, were observed for #4 and its calf (#5) on both days, and were highly significant ($P < 0.001$). Porpoise #52 and its calf (#50) were present on only one of the two sampled days (January 29, 1976), and their association at that time was also highly significant ($P < 0.001$). Except for adult-calf surfacing associations there was no detectable stable relationship in animals surfacing together (Table I) and animals appearing together in subgroups on different days (Fig. 3).

Because all individuals were recognized as they surfaced during the two sampled sessions, dive time data were accumulated as well. Individuals dove for a mean of 21.8 seconds, with little fluctuation from this mean (s.d. = 3.01). The small calf present on January 29, 1976, surfaced slightly more frequently than the overall mean (#50 = 17.8 sec/dive) and slightly more frequently than its presumed mother (#52 = 21.3 sec/dive).

Calving seasonality

Five calves were observed throughout the study, and two were reported after termination of the study (Table II). The mean number of calves per subgroup was 1.5 for the 35 sightings of completely-known groupings to pass by camp. On the average, 10% of a subgroup was composed of calves. Calves were born during

TABLE II

The estimated birthdates of seven calves, arranged by month. The two un-numbered calves were reported first seen in the months shown, after termination of the 21-month study. Note the absence of births May through October.

Months	Estimated dates of calf births
January	# 21 (1975); # 50 (1976)
February	none
March	# 53 (1976); no number (1977)
April	# 5 (1974); no number (1977)
May	none
June	none
July	none
August	none
September	none
October	none
November	# 36 (1974)
December	none

spring, summer, and fall, with no births during winter (June-September). The births of seven calves during the six month period from November through April (see Table II) are nonrandomly clumped toward those months ($P < 0.02$, Raleigh test, Greenwood and Durand, 1955). There was no evidence of births for May through October.

DISCUSSION

Recognized individuals of bottlenose porpoises were found in the study area throughout the year and thus did not migrate with the changing seasons. True (1891) reported that specimens of *Tursiops* off Cape Hatteras, North Carolina, move toward the north in the spring and return south in the fall (see also Mead, 1975). Gunter (1942), however, reports that specimens of *Tursiops* in Texas waters show no seasonal migration; while Caldwell and Caldwell (1972) and Odell (1975) suggest a possible seasonally-related movement of this species off the southern tip of Florida. Apparently some bottlenose porpoise populations migrate and others, at least at times, do not. It is likely that the porpoises go where they can find food, as has been indicated for other species (Evans, 1971; Norris and Dohl, 1978a).

Although there was no evidence for seasonal migration in the Argentine study area, there was a four months cycle in the number of times that porpoises were sighted. Lows occurred in August-September, January-February, and May-June; and highs in July, November, and March. The near-shore surface water temperature in the study area varies from a July-August low of approximately 10.5° C to a January-March high of 17 to 18° C (personal observation). Since lows and highs of bottlenose porpoise presence occurred during both the low and high temperature periods of the year, as well as during intermediate water temperatures, occurrence pattern of this population does not appear temperature-dependent. In other areas of the world, this species is also found over a wide water temperature

range, from approximately 8° C to 30° C (Van Bree, University of Amsterdam, personal communication).

Subgroups which were seen from shore during the 21-month study varied in size and in composition of individuals from sighting to sighting. Nevertheless, five animals of a recognized group of 53 animals were consistently present when a subgroup was sighted. These five individuals were composed of a large adult (#1), two smaller adults (#2 and #3), and an adult (#4) with its calf (#5). Judging by size, it is possible that the large adult, #1, was a male and the other adults were females. This kind of association has been described for bottlenose porpoises in captivity (Tavolga, 1966; Caldwell and Caldwell, 1972), as well as in the wild (Caldwell and Caldwell, 1972; Irvine, University of Florida, personal communication). In the present study this supposition rests only on relative size of individuals and not on known sex.

In addition to the four adults and one calf which were consistently present, six individuals (#7-12) were present until September, 1975; and five individuals (#14-18) were present from September, 1975, to the end of the study. These two stable groupings were composed of all adults, with no calves or juveniles present. Caldwell and Caldwell (1972) hypothesized that such units may be composed of nonbreeding population members. They may travel together as do, for example, bachelor herds of elephants (Douglas-Hamilton and Douglas-Hamilton, 1975), but for the present population this can only be taken as a suggestion, in need of further study.

Perhaps most interesting in the present study was the apparent fluidity with which many individuals appeared and disappeared, causing a constant fluctuation in subgroup size and composition. These individuals were composed of adults of varying sizes, and of calves and juveniles. A similar situation in group size fluctuation exists in the Hawaiian spinner porpoise, *Stenella longirostris* (Norris and Dohl, 1978b). A possibly similar system in Florida bottlenose porpoises has been observed recently by Wells and Irvine (University of Florida, personal communication) and may be found to be quite common in coastal porpoise species as further population studies are made.

Such a fluidity in sturture surpasses the individual interchanges between known "open" groups of most terrestrial mammals (Wilson, 1975, pages 456-546). To conform to the standard notion of groups as relatively stable units, the 53 known individuals of the present population have been labeled *group*, while the units that periodically came by shore, consisting of 8 to 22 animals, have been termed *subgroups* (Würsig and Würsig, 1977). These flexible subgroups appear similar to the casual units found in chimpanzee (*Pan troglodytes*) society (Goodall, 1965; Reynolds and Reynolds, 1965; Hall, 1968; Nishida, 1968; Sugiyama, 1968). The possibility of similarity in group organization between *Tursiops* and *Pan* was first suggested by Tayler and Saayman (1972b). In chimpanzee society, it appears that this constant fluctuation in subgroup size is in direct response to irregular and patchy food availability, with small units when food is being sought and larger units in areas of greater food abundance (Reynolds, 1965). It is suggested that food availability may also be a primary determinant of subgroup size and stability in the present bottlenose porpoise population.

Because this study relied on sightings at a discrete point along the shoreline, little information about the group's total range was gathered. At least at times some of the animals travelled unexpectedly long distances, however. Six individuals were identified in a bay south of Golfo San José, separated from camp by over 300 kilometers, and nine months later four of these animals were again found near camp. Either the normal range of this population extends over so extensive a distance, or the individuals so observed had crossed into the new area. Similar distances travelled have been reported for pelagic porpoises (Perrin, 1975; Evans, 1974), but not for nonmigrating near-shore species.

Although some adult porpoises showed a tendency to surface together, this is not a long-term relationship and may shift from day to day. Just as terrestrial animals which have formed close social bonds do not in general exhibit synchronized breathing, porpoises not surfacing together may still be closely associated. However, porpoises, unlike terrestrial animals, must leave their underwater positions while surfacing to take a breath. As a result, very close animal associations may be reflected in the breathing-surfacing pattern. This appears to be the case in adult-calf associations. Porpoise #4 and its calf (#5) and #52 and its calf (#50) often surfaced together. In the #4-calf association, this relationship was still strong in December, 1976, approximately two and one-half years after #4's calf was born. Nevertheless, such association is not absolute. As the increased surfacing rate of #50 (17.8 sec/dive) over that of its presumed mother (#52 = 21.3 sec/dive) shows, the calf at times surfaced independently of the adult. When it did so, it was almost always seen moving ahead of the subgroup of animals, an apparently investigative or "play" behavior summarized for other species by Norris and Dohl (1978a). While Caldwell and Caldwell (1972) reported the same type of non-association to be present at times in captive porpoises, Irvine (University of Florida, personal communication) believes that it does not occur in a bottlenose porpoise population in the Sarasota-Bradenton area of central west Florida. A possible explanation of this difference in behavior may be the relatively undisturbed state of porpoises in the present study, unlike Florida populations which have been harassed by capture vessels and tourist boats. Thus, Florida porpoises may keep their young within the confines of the school during periods of possible danger such as the approach of a boat, while no such restriction appeared to apply to porpoises in Golfo San José. Instead, calves and subadults at times briefly left the side of the adult with which they normally surfaced and approached the investigator's boat without apparent caution.

Since bottlenose porpoises have an approximately 12-month gestation period (Sergeant, Caldwell, and Caldwell, 1973), the marked summer calving season within the present population also indicates an increase in mating activity at that time. Various investigators (Mead, 1975; Odell, 1975; Sergeant, Caldwell, and Caldwell, 1973; Evans, Navy Underwater Center, San Diego, personal communication, for *Delphinus delphis*; Nishiwaki, Nakajima, and Kamiya, 1965, and Harrison, Brownell, and Boice, 1972, for *Stenella attenuata*) have reported a tendency toward bimodal calving, with peaks in spring and fall. Ridgway and Green (1967) found anatomical evidence for mating peaks in spring and fall by an increase in testes weights of male *Delphinus delphis* and *Lagenorhynchus obliquidens* during these

two seasons. The present population may exhibit a similar mating and calving trend, with one calf first observed in November, and six others first seen from January through April. Why a bimodal calving peak appears to be present in various different species of toothed cetaceans is not known. In the present study, the late summer calving preference coincides with the highest water temperatures of the year. This higher ambient temperature, as in most terrestrial mammals and in pinnipeds and baleen whales, may be of physiological advantage to the newly-born young.

The present study demonstrates that by systematically photographing small groupings of coastal porpoises much can be learned about their organization and dynamics. This represents one of the first times that such an attempt has been reported (see also Würsig and Würsig, 1977), and it is hoped that more such studies, on different odontocete cetacean populations and on different species, will soon be made. In this manner, by observing coastal porpoises for long periods of time, long-overdue descriptions of natural populations—analogueous to the recent flowering of primate research—may take place.

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SUMMARY

1. During a 21-month study, individuals of *Tursiops truncatus* in Golfo San José, Argentina, exhibited a four month occurrence cycle, but showed no seasonal migration.

2. Subgroups numbering 8 to 22 animals included a small core unit of individuals which were consistently found together. Other animals appeared and disappeared in these subgroups on different days in a highly fluid manner which paralleled the open society of African chimpanzees, *Pan troglodytes*.

3. Some adults showed weak and changing surfacing associations with other adults. Calves consistently surfaced together with a particular adult, except during apparent play or investigative behavior, when calves left adults for brief periods. The mean dive time per animal was 21.8 seconds.

4. Six of seven calves were born in late summer. This calving peak coincided with the highest water temperatures of the year.

LITERATURE CITED

- CALDWELL, D. K., AND M. C. CALDWELL, 1972. *The world of the bottlenosed dolphin*. J. B. Lippincott Press, Philadelphia and New York, 157 pp.
- DOUGLAS-HAMILTON, I., AND O. DOUGLAS-HAMILTON, 1975. *Among the elephants*. Viking Press, New York, 284 pp.
- EVANS, W. E., 1971. Orientation behavior of delphinids: radio telemetric studies. *Ann. N. Y. Acad. Sci.*, **188**: 142-160.
- EVANS, W. E., 1974. Radio-telemetric studies of two species of small odontocete cetaceans. Pages 386-394 in W. Scheyll, Ed., *The whale problem; a status report*. Harvard University Press, Cambridge, Massachusetts.
- GOODALL, J., 1965. Chimpanzees of the Gombe Stream Reserve. Pages 425-473 in I. DeVore, Ed., *Primate behavior*. Holt, Rinehart, and Winston, New York.
- GREENWOOD, J. A., AND D. DURAND, 1955. The distribution of length and components of the sum of n random unit vectors. *Ann. Math. Stat.*, **26**: 233-246.
- GUNTER, G., 1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. *J. Mammal.*, **23**: 267-276.
- HALL, K., 1968. Social organization of the old-world monkeys and apes. Pages 7-31 in P. Jay, Ed., *Primates: studies in adaptation and variability*. Holt, Rinehart, and Winston, New York.
- HARRISON, R. J., R. L. BROWNELL, JR., AND R. C. BOICE, 1972. Reproduction and gonadal appearances in some odontocetes. Pages 361-429 in R. J. Harrison, Ed., *Functional anatomy of marine mammals, Vol. 1*. Academic Press, New York.
- MEAD, J. G., 1975. Preliminary report on the former net fisheries for *Tursiops truncatus* in the western north Atlantic. *J. Fish. Res. Board Can.*, **32**: 1155-1162.
- MITCHELL, E., 1975. *Porpoise, dolphin, and small whale fisheries of the world*. Unwin Brothers, Surrey, England, pages 30-101.
- NISHIDA, T., 1968. The social group of wild chimpanzees in the Mahali mountains. *Primates*, **9**: 175-198.
- NISHIWAKI, M., M. NAKAJIMA, AND T. KAMIYA, 1965. A rare species of dolphin (*Stenella attenuata*) from Arari, Japan. *Sci. Rep. Whales Res. Inst. (Tokyo)*, **19**: 53-64.
- NORRIS, K. S., 1974. *The porpoise watcher*. W. W. Norton, New York, 250 pp.
- NORRIS, K. S., AND T. P. DOHL, 1978a. The structure and functions of cetacean schools. In press in L. Herman, Ed., *Cetacean behavior*. Wiley Interscience, New York.
- NORRIS, K. S., AND T. P. DOHL, 1978b. The behavior of the Hawaiian spinner porpoise, *Stenella longirostris*. *U. S. Natl. Mar. Fish. Serv. Fish. Bull.*, in press.
- ODELL, D. K., 1975. Status and aspects of the life history of the bottle nose dolphin, *Tursiops truncatus*, in Florida. *J. Fish. Res. Board Can.*, **32**: 1055-1058.
- PERRIN, W. F., 1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. *J. Fish. Res. Board Can.*, **32**: 1059-1067.
- REYNOLDS, V., 1965. Some behavioral comparisons between the chimpanzee and the mountain gorilla in the wild. *Am. Anthropol.*, **67**: 691-706.
- REYNOLDS, V., AND F. REYNOLDS, 1965. Chimpanzees of the Budongo Forest. Pages 368-424 in I. DeVore, Ed., *Primate behavior*. Holt, Rinehart, and Winston, New York.
- RIDGWAY, S. H., AND R. F. GREEN, 1967. Evidence for a sexual rhythm in male porpoises, *Lagenorhynchus obliquidens* and *Delphinus delphis bairdi*. *Nor. Hvalfangst-tidende*, **1**: 1-8.
- ROHLF, F. J., AND R. R. SOKAL, 1969. *Statistical tables*. W. H. Freeman, San Francisco, 253 pp.
- SAAYMAN, G. S., D. BOWER, AND C. K. TAYLER, 1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. *Koedoc*, **15**: 1-24.
- SERGEANT, D. E., D. K. CALDWELL, AND M. C. CALDWELL, 1973. Age, growth, and maturity of bottlenosed dolphins (*Tursiops truncatus*) from north-east Florida. *J. Fish. Res. Board Can.*, **30**: 1009-1011.
- SOKAL, R. R., AND F. J. ROHLF, 1969. *Biometry*. W. H. Freeman, San Francisco, 776 pp.
- SUGIYAMA, Y., 1968. Social organization of chimpanzees in the Budongo Forest, Uganda. *Primates*, **9**: 225-258.

- TAVOLGA, M. C., 1966. Behavior of the bottlenose dolphin (*Tursiops truncatus*): social interactions in a captive colony. Pages 718-730 in K. Norris, Ed., *Whales, dolphins, and porpoises*. University of California Press, Los Angeles.
- TAYLER, C. K., AND G. S. SAAYMAN, 1972a. A method for determining the composition, deployment, and stability of free-ranging dolphins. *Z. Säugetierkd.*, **37**: 116-119.
- TAYLER, C. K., AND G. S. SAAYMAN, 1972b. The social organization and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. *Ann. Cape Prov. Mus. Nat. Hist.*, **9**: 11-49.
- TRUE, F. W., 1891. Observations on the life history of the bottlenose porpoise. *U. S. Natl. Mus. Proc.*, **1890**: 197-203.
- WILSON, E. O., 1975. *Sociobiology, the new synthesis*. Harvard University Press, Cambridge, Massachusetts, 697 pp.
- WÜRSIG, B., AND M. WÜRSIG, 1977. The photographic determination of group size, composition, and stability of coastal porpoises, *Tursiops truncatus*. *Science*, **198**: 755-756.